

REVISION OF *DESMOMETOPA* LOEW (*LITOMETOPA* SABROSKY)
(DIPTERA: MILICHIIDAE), WITH DESCRIPTIONS OF SIX NEW SPECIES

I. BRAKE AND A. FREIDBERG

(IB) Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany (e-mail: i.brake.zfmk@uni-bonn.de); (AF) Department of Zoology, The George S. Wise faculty of Life Sciences, Tel Aviv University, Tel Aviv 69978, Israel (e-mail: afdipter@post.tau.ac.il)

Abstract.—The Afrotropical genus *Litometopa* Sabrosky is relegated to subgeneric status within *Desmometopa* Loew and revised. *Desmometopa* (*L.*) *glabrifrons* (Sabrosky), the type species, is redescribed, and six new species, *D. (L.) brachycephala*, *D. (L.) dolichocephala*, *D. (L.) flavicornis*, *D. (L.) glandulifera*, *D. (L.) nigrifemorata*, and *D. (L.) sabroskyi*, are described. The subgenus is redescribed, including a description of sclerotized structures within the male abdomen possibly representing a gland, and a specialization of the female ovipositor, known as the secondary ovipositor. A key to all species is given. The relationship between *Litometopa* and other taxa within *Desmometopa* and among species of *Litometopa* is discussed.

Key Words: Diptera, Milichiidae, *Desmometopa* (*Litometopa*), new status, Afrotropical

In 1965 Sabrosky established the genus *Litometopa* for his new species, *L. glabrifrons* Sabrosky, based on four specimens collected in Tanzania. The genus was not recorded again until Brake (2000) discussed it in her study of the Milichiids. Although museum specimens are relatively scarce, about 130 recently have become available to us, including six new species, which are described herein.

In his description of *Litometopa*, Sabrosky stated that *Litometopa* is closely related to *Desmometopa* Loew and wrote: "In a sense, it [*Litometopa*] is an extreme form of the latter [*Desmometopa*], with interfrontal hairs and stripes absent, and orbital bristles and mesonotal hairs greatly reduced." In his revision of *Desmometopa*, Sabrosky (1983) recorded several polished black species, which were intermediate between *Desmometopa* and *Litometopa* in that they shared most (plesiomorphic) characters of

Desmometopa but lacked the (apomorphic) interfrontal stripes. He mentioned the possibility that these were degrees of reduction from the interfrontal stripes of *Desmometopa* but preferred to retain the distinctness of the stripes as uniquely characteristic of *Desmometopa*. According to the phylogenetic study of *Litometopa* and *Desmometopa* present in this paper, *Litometopa* is closely related to some *Desmometopa* species and is part of this genus. Therefore, we include *Litometopa* as a subgenus of *Desmometopa*. Based on new characters, the subgenus *Litometopa* and its type species, *D. (Litometopa) glabrifrons* (Sabrosky), are redescribed. In her key to genera of Milichiidae Brake (2000) pairs *Litometopa* with the branch leading to *Desmometopa*, *Lepitometopa* Becker, and *Madiza* Fallén, differing by the presence of only one orbital seta and by the absence of interfrontal setulae, except for an anterior pair. The iden-

tification of species of *Litometopa* is in some cases quite difficult, because, while they do not differ in male or female terminalia, leg coloration and the shape of the head do differ but these characters are somewhat variable. As an added complication, the shape of the head is sexually dimorphic.

Future research on *Litometopa* should include histological sections of the male abdomen, which contains sclerotized reservoirs of possible glandular function.

The terminology essentially follows McAlpine (1981) with a few exceptions. We follow White et al. (2000) in using "microtrichia" instead of McAlpine's "pruinose," because the body surface is covered with microscopic outgrowth of the cuticle and not with dust or a waxy substance (pruinose). For the vertical setae we use the terms "medial" and "lateral" (White et al. 2000) instead of the traditional "inner" and "outer," respectively. The terminology of the prothorax follows Speight (1969), and that of the male genitalia Cumming et al. (1995). The definition of "dark" is brown and black. Descriptions are composite. For the most part information given in the description of the genus is not repeated in the species descriptions.

We thank the following curators and institutions for lending specimens.

HU	Museum für Naturkunde der Humboldt Universität, Berlin, Germany (Dr. M. Kotrba)
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany (Dr. H.-P. Tschorsch)
TAU	Tel Aviv University, Tel Aviv, Israel
UBI	Fakultät für Biologie, Universität Bielefeld, Bielefeld, Germany (Dr. M. von Tschirnhaus)
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (Dr. W. N. Mathis)

Some paratypes will be deposited in the

following institutions (as well as the USNM):

BM	The Natural History Museum, London, U.K.
NMWZ	National Museum and Galleries of Wales, Cardiff, U.K.
ZFMK	Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany
ZSM	Zoologische Staatssammlung München, Germany

Desmometopa subg. *Litometopa*
Sabrosky, **new status**

Litometopa Sabrosky 1965: 4.

Type species: *Litometopa glabrifrons* Sabrosky. Original designation.

Description.—*Head* (Figs. 4–5, 7–8, 10–11): About as long or longer than high, black, only base of arista and often base of palpus yellowish, polished except for microtrichose antenna, fovea, and ventral facial margin. Frons glabrous, polished, 1.3–2.0× as long as broad (length measured from pitinal fissure to base of postocellar setae; breadth measured at narrowest point between eye margins). Frontal width nearly equal in male and female (Fig. 10); lacking interfrontal stripes or setulae, except pair of setulae anteriorly. Frontal triangle small, not extended beyond ocelli. One reclinate and slightly latero-clinate orbital seta and 2 medio-clinate frontal setae. Two proclinate setulae between orbital seta and posterior frontal seta, anterior seta slightly larger than posterior one, possibly representing reduced anterior orbital seta. One medio-clinate setula present close and anterior to posterior frontal seta, and one medio-clinate setula present anterior to anterior frontal seta. Latero-proclinate ocellar and medial and lateral vertical setae present. Postocellar setae parallel to slightly convergent. Lunule visible, extended to basal part of first flagellomere, triangular, pointed, with pair of setulae. Face concave, antenna short, first flagellomere round; arista long, slender, microscopically pubescent. Vibrissal angle produced,

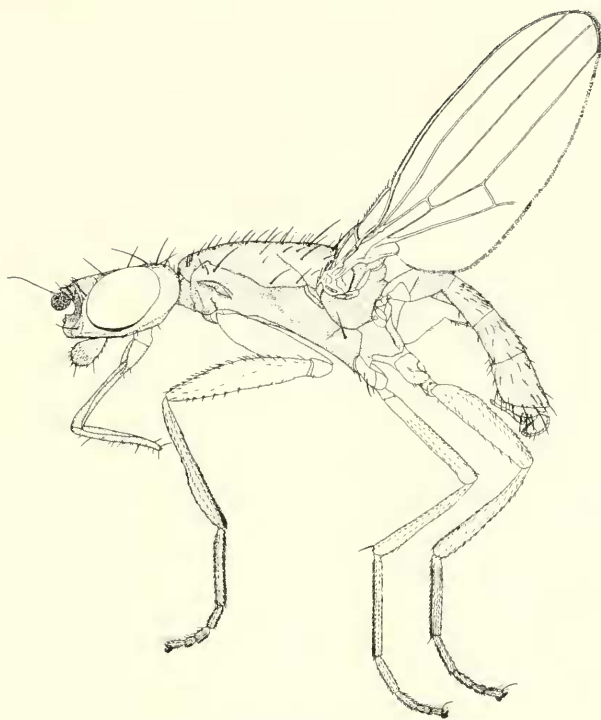


Fig. 1. *Desmometopa dolichocephala*, male, habitus (after Brake 2000).

usually half as broad as first flagellomere, but sometimes equibroad or broader (vibrissal angle measured from anteriormost point of eye margin to anterior tip of vibrissal angle), vibrissa well developed. Gena about 0.1–0.2 \times as high as eye. Post-orbital region (i.e., space between eye and postocular setulae) in male 2–3 \times longer than in female, up to about a third as long as eye (Fig. 4) (length of eye measured as horizontal line between anteriormost and posteriormost points of eye; length of post-orbital region measured at posteriormost point of eye). Palpus flat, elongate spatulate to rather broad (Figs. 6, 9), with small setulae and two longer setae at anterolateral

edge; in male entirely microtrichose, in female ventrally glabrous and shiny. Clypeolabral membrane at base of palpus slightly sclerotized. Prementum broader and thicker than combined labella, which have four pseudotracheae each. In female, pseudotracheal teeth on medial pseudotrachea extremely long and thin (Fig. 20, arrow), bent to about 90 $^\circ$, and with small subsidiary tooth at angle. Small subsidiary teeth also present on teeth of other pseudotracheae. In male, teeth on all pseudotracheae about equally long and neither bent nor toothed (Fig. 19).

Thorax: Black, narrow and elongate (Fig. 1). Mesonotum 1.5–2.0 \times as long as

broad, finely shagreened, subshiny, almost bare of setulae, with only dorsocentral row of setulae and median (unpaired) acrostichal row, that becomes 2 irregular rows posteriorly, and few scattered setulae laterally. Anepisternum and furcasternum elongate and fused. Basisternum with precoxal bridge, similar to variant "QT" of Speight (1969) (Fig. 12). Pleura strongly shiny, though in part somewhat rugose, anepimeron and katapisternum posteriorly and meron, katatergite and anatergite entirely dull, gray microtrichose. Scutellum shiny, glabrous. Chaetotaxy: 1 long postpronotal seta and 2 postpronotal setulae, of which one may be longer and directed dorsad, 2 notopleural setae, 1 presutural represented by setula, 1 short supraalar, 1 long postalar, 1 short intraalar, 2 dorsocentral setae, anterior one about half length of posterior one, and row of dorsocentral setulae progressively shortened anteriorly, 1 apical and 1 basal scutellar setae, basal seta $\frac{1}{2}$ as long as apical seta, anepisternum bare, 1 katapisternal and no anepimeral seta.

Legs: Foreleg large, appearing raptorial, with elongate coxa and often incrassate femur with anteroventral and posteroventral rows of 6–8 strong spines each (Fig. 1). Forecoxa bright yellow, and foretibia and foretarsus black in all studied species, whereas forefemur varies between species, from predominantly black to almost entirely yellow. Foreleg appears thicker due to brush of black setulae ventrally at distal end of tibia and on tarsus. Mid- and hindlegs more or less normal. Mid- and hindtibiae and mid- and hindtarsi except distal tarsomeres yellow. Basal two tarsomeres of hindleg with posteroventral brush of either pale (yellow) or dark (brown or black) setulae. Pale setulae more coarsely and more spirally fluted than normal black setulae in *D. brachycephala* (Fig. 21). Structure of setulae in brush not studied in other species.

Wing: Hyaline. R_{4+5} and M_{1+2} very slightly convergent (Fig. 13). Last section of M_{1+2} about $2.75\times$ as long as penultimate

section. Cell cup closed, but only weakly differentiated.

Abdomen: Black, slender and elongate. Male usually with paired sclerotized internal saclike structures (see next section). Male terminalia similar to those of other *Desmometopa* species. Cercus as large as epandrium in lateral view (Fig. 17); 2–4 long setae laterally on epandrium, number sometimes varying between sides. Surstylus partly fused to epandrium, covered by setulae medially (Fig. 18), similar to flame of candle in ventral view. Pregonite with 2 setulae distally. Distiphallus forming long membranous tube, which is widened in middle, dorsobasally with sclerotized strip.

Female with tergite and sternite 6 and 7 not reduced in size (reduced in many other Milichiidae). Lateral margins of sternite 7 and tergite 7 overlapping (Fig. 22). Sternite 6 anteromedially with small pointed process (Fig. 16). Segment 7 internally with secondary ovipositor (Brake 2000; and see next section). Female internal reproductive system without any sclerotized structures. Spermathecal ducts elongated and loosely (i.e., the ducts are not lying directly next to each other) rolled together distally into one small coil. Spermathecal duct basally wider and possibly surrounded by muscles. Duct and surrounding epithelium in coil narrower. No sclerotized spermathecal capsule. Distal end of spermathecal duct projecting out of coil and surrounded by epithelial gland cells. Tip of duct slightly enlarged (see fig. 24H, *D. sabroskyi*, in Brake 2000).

Peculiarities of the male and female genitalia.—Males of *Litometopa* usually have peculiar paired structures within the fifth abdominal segment (Fig. 14). Each structure consists of two sclerotized reservoirs, which are surrounded by tissue. The reservoirs are elongate sacs connected by ducts, which are sclerotized in the same manner. The duct leading to the anterior reservoir is longer than the one leading to the posterior reservoir. The ducts lie dorsally, but the sacs are directed ventrad. Near the terminalia, the ducts of both reservoirs meet and

fuse to form a common duct. The common ducts of either side open close to each other dorsally between the fifth tergite and the terminalia. On each common duct there is a spiracle, probably spiracle 7. A second spiracle lies in the membrane between the duct opening and the fifth tergite. This is probably the spiracle 6. There does not seem to be a valve for the reservoirs. The sclerotized wall of the reservoirs is covered by slight, longish indentations, similar to the surface of a golfball. A few short setulalike structures are on these indentations towards the lumen of the reservoir. It is possible that each of these structures represents a connection between the surrounding tissue and the reservoir. However, in SEM dissections no holes in the tip of the setulalike structures could be discerned. The reservoirs in all dissected specimens (both dry and alcohol-preserved material) seemed to be empty. We suppose that this structure represents a gland, based on the tissue surrounding the reservoirs and on the setulalike structures in the reservoirs. We will use the term "abdominal reservoirs" for this structure. The abdominal reservoirs possibly evolved from synsternite 7/8, which is absent in *Litometopa*, because the 6th and 7th spiracle are often in synsternite 7/8 in Milichiidae and especially in *Desmometopa*.

In females there is a specialized structure inside segment 7, which is called a secondary ovipositor and is used for oviposition (Fig. 15) (Brake 2000). Presumably, while ovipositing, the secondary ovipositor is everted telescopelike between sternite 7 and the subanal plate. Basally the structure consists of a broad membranous ring with many anteriorly directed barbed spines. Distally there are two weakly sclerotized strips each with a row of yellow setulae. These strips originate ventrolaterally and meet dorsally at the functional tip of the ovipositor. Between these strips, which represent sternite 8, lies the genital opening. When the secondary ovipositor is retracted, only the basal part is turned over, with the

barbed spines now directed posteriorly. In addition to the secondary ovipositor, *Litometopa* is characterised by a very small tergite 8, a bare supra-anal plate and short, round cerci. This combination of characters is not restricted to the subgenus *Litometopa*, but is found in *Desmometopa* species and in *Pholcomyia* and is therefore probably plesiomorphic.

Distribution.—Afrotropical (Fig. 2): Ethiopia, Kenya, Tanzania, Uganda, Rwanda, Congo, Nigeria, and South Africa. This apparently disjunct pattern indicates a possibly wider and more homogenous distribution in the Afrotropical Region.

Biology.—Nothing is known about the biology of *Litometopa* species. Most specimens were swept with a net from flowers, savanna trees and bushes, and some specimens were sampled by canopy fogging.

Since sclerotized reservoirs are found in the abdomen of males only, it is possible that they represent glands that produce sex pheromones. Abdominal glands are quite rare in Diptera. Hennig (1973) gives an overview of the known cases. If only present in one sex, glands were found mostly in females, for example in Phoridae, Lauxaniidae, and some Tephritidae. However in other Tephritidae, Chloropidae (*Thaumatomyia notata* Meigen), and Milichiidae (*Madiza glabra* Fallén) glands were found only in males. These glands have no similarity to the abdominal reservoirs in *Litometopa*, because they are not sclerotized. The only record of sclerotized glandlike structures is from Empididae (Smith and Davies 1964). However, in contrast to *Litometopa*, the two pairs of abdominal organs of males of *Austrodrapetis* lie beneath the third and fourth tergite and have no apparent opening to the surface. Rectal glands are known from Sepsidae, Tephritidae, and Coelopidae and were shown to have a defensive function in Sepsidae (Meier and Dettner 1998).

Cladistic analysis.—The data set for the computer-based cladistic analysis comprises 19 characters and 13 taxa, including 12 spe-

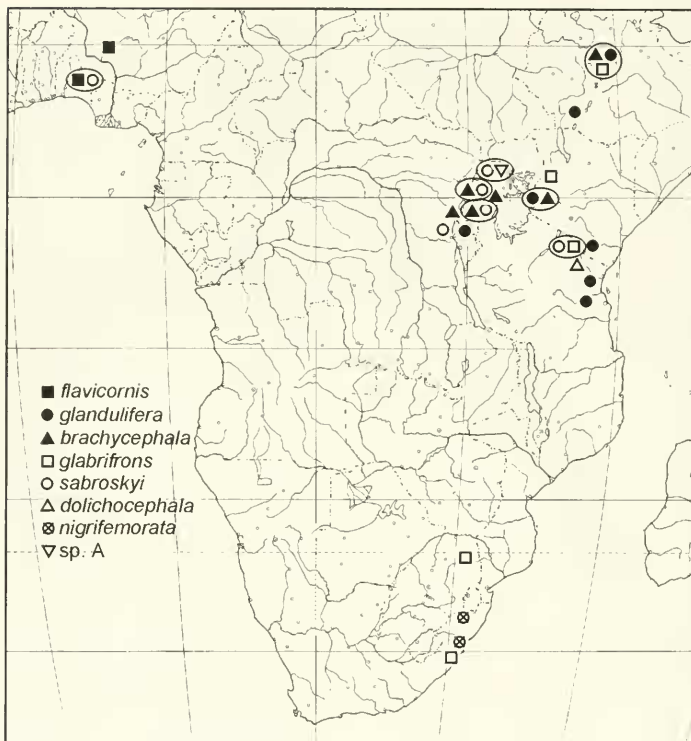


Fig. 2. Distribution records of *Desmometopa* (*Litometopa*) in Africa.

cies of *Desmometopa* and the stem-species pattern of Milichiidae as an outgroup. *Desmometopa m-nigrum* Zetterstedt is a representative of the subgenus *Desmometopa* Loew; *D. tarsalis* Loew, *D. floridensis* Sabrosky, *D. meridionalis* Sabrosky, and *D. melanderi* Sabrosky are representatives of the subgenus *Platophrymia* Williston of *Desmometopa*, and the other species belong to the subgenus *Litometopa* Sabrosky. All characters were treated as unordered. The cladistic analysis was carried out using the exhaustive search option "ie" of Hennig86, which finds the most parsimonious cladogram(s). The precise character distribution can be seen in the data matrix (Table 1).

HEAD

1. Interfrontal stripes: (0) not present; (1) present. In *Desmometopa* and some *Phleomyia* and *Phyllomyza* species, the row of interfrontal setulae is emphasized by sclerotizations at the base of the setulae and the development of microtrichia. In such cases the rows are called interfrontal stripes. Interfrontal stripes are the only known apomorphic character for the genus *Desmometopa* (Sabrosky 1983).
2. Posterior orbital seta: (0) present; (1) absent. According to Brake (2000) the small medio-reclinate seta posterior to

Table 1. Character matrix for species of *Desmometopa* (*Litometopa*) and outgroup.

	1	2	3	4	5	6	7	8	9	10
Stem-species pattern of Milichiidae	00000	02000	00000	0020						
<i>D. (D.) m-nigrum</i>	10000	00000	00000	0000						
<i>D. (P.) tarsalis</i>	10000	11000	00000	0010						
<i>D. (P.) floridensis</i>	10000	11000	00110	0010						
<i>D. (P.) meridionalis</i>	10000	11100	00110	0010						
<i>D. (P.) melanderi</i>	10000	11100	00010	0010						
<i>D. (L.) dolichocephala</i>	01101	11111	10110	1101						
<i>D. (L.) glabrifrons</i>	01111	10011	11110	1100						
<i>D. (L.) glandulifera</i>	01111	11011	10110	1001						
<i>D. (L.) sabroskyi</i>	01111	10011	11110	1101						
<i>D. (L.) flavicornis</i>	01111	10011	11100	1101						
<i>D. (L.) nigrifemorata</i>	01110	11111	10110	1000						
<i>D. (L.) brachycephala</i>	01111	10011	10110	1101						

the large laterocline orbital setae in *Desmometopa* is homologous to the posterior ("upper") orbital seta in the stem-species pattern of Milichiidae. This seta is apomorphically absent in *Litometopa*.

- Middle orbital seta: (0) laterocline; (1) latero-recline. As discussed above, the posterior orbital seta in *Litometopa* is absent. Therefore the posteriormost orbital seta in this subgenus is probably homologous to the middle orbital seta in the stem-species pattern of Milichiidae (Brake 2000). A change in the inclination of the middle orbital seta from laterocline and only slightly reclinate to mainly reclinate and only slightly laterocline occurred several times within the Milichiidae and is apomorphic for *Litometopa*. The anterior orbital seta in *Litometopa* is possibly represented by the anterior of two setulae between middle orbital seta and frontal setae.
- Anterior frontal seta: (0) 0.66–1.00× as long as posterior frontal seta; (1) about half as long as posterior frontal seta. In Milichiidae the frontal setae usually have the same length.
- Setulae between frontal setae: (0) two;

(1) one. The number of setulae between the frontal setae in Milichiidae is often two. In *Desmometopa* the number is two in all studied species of the subgenera *Desmometopa* and *Platophrymia*. Therefore the presence of only one setula is considered to be apomorphic.

- Face: (0) not concave; (1) concave. The comparatively protuberant ventral margin of the head and deeply concave face as seen in profile, is one of the characters Sabrosky (1983) used to separate the subgenus *Platophrymia* from the subgenus *Desmometopa*, in which the face is only slightly concave. Since the face is only slightly concave in most Milichiidae, this character state is supposed to be plesiomorphic.
- Palpus coloration in male: (0) basally yellow; (1) entirely black. The coloration of the palpus varies within Milichiidae and within *Desmometopa*. Therefore the polarity of this character is unknown.
- Palpus shape in male: (0) not enlarged; (1) enlarged. In the stem-species pattern of Milichiidae the palpus is short and clavate. The shape of the palpus in several *Desmometopa* species differs from the stem-species pattern in that it is slightly longer with the width a third of the vertical eye diameter or more. Within *Desmometopa* an enlarged palpus occurs in two species of the subgenus *Desmometopa* and in less than half of the species of *Platophrymia*.
- Palpus microtrichia in female: (0) entirely microtrichose; (1) polished ventrally. In all Milichiidae we studied (for list of studied species see Brake 2000), including members of *Desmometopa*, the palpus is entirely microtrichose. Therefore a ventrally polished palpus is considered apomorphic.

THORAX

- Presutural seta: (0) as long as or longer than supraalar seta; (1) shorter than su-

praalar seta. The size reduction of the presutural seta is apomorphic for *Litometopa*.

11. Mesonotum setulation: (0) with many setulae; (1) almost bare of setulae except for dorsocentral row of setulae and median (unpaired) acrostichal row, that becomes two irregular rows posteriorly, and few scattered setulae laterally. In all Milichiidae we studied, the mesonotum is covered by many acrostichal setulae. The reduction of the number of acrostichal setulae is therefore considered apomorphic for *Litometopa*.
12. Suture between anepisternum and furcasternum (0) present; (1) absent. In all Milichiidae we studied, the suture between anepisternum and furcasternum is present. The absence of this suture is therefore considered apomorphic for *Litometopa*.

LEGS

13. Forecoxa coloration: (0) black; (1) yellow. In most Milichiidae all coxae are black. However, the forecoxa is yellowish in several species of *Neophylomyza* and *Leptometa*.
14. Forecoxa: (0) not elongate; (1) elongate. In *Litometopa* and *Platophrymia* the thorax and forecoxa are elongate, especially in relation to the height of the thorax at the base of the coxa.
15. Forefemur coloration: (0) black; (1) slightly yellow at base; (2) basal 0.25–0.60 yellow; (3) almost entirely yellow except for anterodorsal brown stripe distally. In most Milichiidae, including members of *Desmometopa*, the forefemur is black. Therefore a yellow forefemur is considered apomorphic.
16. Midfemur and hindfemur coloration, except for apices: (0) black; (1) yellow. In most Milichiidae, including members of *Desmometopa*, the midfemur and hindfemur are black. Therefore yellow mid- and hindfemora are considered apomorphic.
17. Apices of midfemur and hindfemur: (0)

black; (1) yellow. Dark legs with yellow apices of the midfemur and hindfemur are known in several species of Milichiidae, but seem to have evolved several times independently. As the apices are black in all studied species of the subgenera *Desmometopa* and *Platophrymia*, yellow apices are considered to be apomorphic.

18. Posteroventral brush on hindtarsus: (0) black or brown; (1) yellow. The coloration of this brush varies within Milichiidae, and the polarity of this character is unknown.

ABDOMEN

19. Sclerotized reservoirs in male abdomen: (0) absent; (1) present. Sclerotized reservoirs are unique to *Litometopa* and have neither been found in other Milichiidae, nor in other acalyptrate flies.

The cladistic analysis found 48 most parsimonious trees of 32 steps (consistency index: 0.65; retention index: 0.86). The Nelson tree of these 48 trees is depicted in Fig. 3.

Discussion (numbers in square brackets refer to the characters used in the cladistic analysis).—*Litometopa* is closely related to *Desmometopa* (*Platophrymia*) (Sabrosky 1965, 1983), sharing the shiny black lateroventral corner of the facial plate, immediately mesad of the vibrissal angle and the concave face [6] (Brake 2000). However, there are two rows of strong spines on the forefemur in *Litometopa*, but only one anteroventral row of weak spines in these *Platophrymia* species. Within *Platophrymia*, *Litometopa* is most closely related to the group around *D. floridensis*, *D. melanderi*, and *D. meridionalis*, sharing the enlarged palpus [8] and the elongated yellow [13, 14] forecoxa and often incrassate forefemur. However, *Litometopa* is Afrotropical, whereas the related *Platophrymia* spp. are Nearctic or Neotropical. The close relationship between *Litometopa* and some *Plato-*

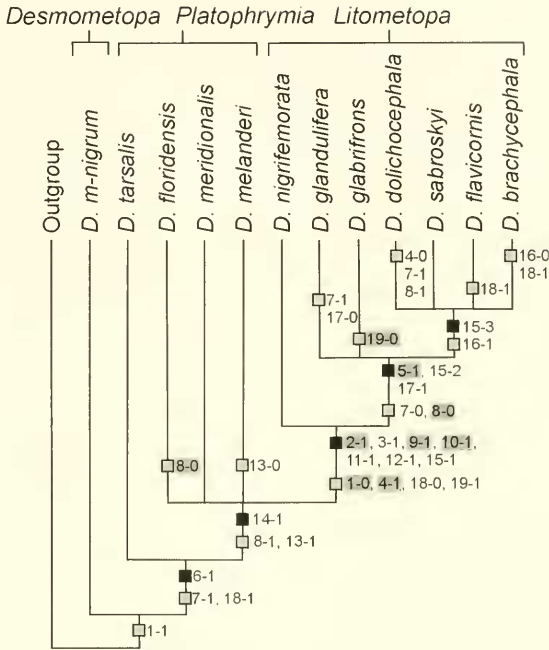


Fig. 3. Phylogenetic tree of *Desmometopa* subgenera: shaded hatchmarks indicate character changes that either reverse or evolved at least twice on the tree; black hatchmarks indicate changes that do not reverse and evolved only once; reductions are marked with a dark shading.

phrymia species results in a paraphyly of *Platophrymia*. However, we have decided to keep both subgenera separate, as they are easily recognisable and differ from each other in several characters, and a more rigorous phylogenetic study of *Platophrymia* and of the whole genus *Desmometopa*, which would clarify the presence of monophyletic groups within the genus, is still needed.

The subgenus *Litometopa*, as diagnosed above, is clearly a monophyletic group. Its apomorphies are: [2] posterior orbital seta lost (plesiomorph: present); [3] middle orbital seta (in *Litometopa* the actual posterior seta) reclinate (plesiomorph: latero-clinate); anterior orbital seta reduced in size (ple-

siomorph: as large as the other orbital setae); [9] female palpus polished ventrally (plesiomorph: palpus entirely microtrichose); [10] presutural seta reduced in size (plesiomorph: not reduced); [11] mesonotum almost bare of setulae (plesiomorph: covered with setulae); [12] suture between anepisternum and furcasternum lost (plesiomorph: present); and probably also [19] the presence of abdominal reservoirs in males (plesiomorph: not present), though the state of this character is unknown for *D. nigrifemorata*.

Within *Litometopa*, the yellow forefemur [15–3] is the synapomorphic character of a clade comprising *D. brachycephala*, *D. dolichocephala*, *D. flavicornis*, and *D. sabros-*

kyi. These four species together with *D. glabrifrons* and *D. glandulifera* form a clade that is supported by the following apomorphic characters: only one setula present between frontal setae [5–1], basal 0.25–0.60 of forefemur yellow [15–2], and apices of mid- and hindfemora yellow [17–1].

KEY TO SPECIES OF *DESMOMETOPA*
(*LITOMETOPA*)

1. Posteroventral brush of hindtarsus yellow 2
- Posteroventral brush of hindtarsus black or brown 4
2. Mid- and hindfemora black. Male with first flagellomere black 4
- *D. (L.) brachycephala*, new species
- Mid- and hindfemora yellow. Male with first flagellomere yellowish medially and basally 3
3. Male with postorbital region about $\frac{1}{6}$ as long as eye *D. (L.) flavicornis*, new species
- Male with postorbital region about $\frac{1}{10}$ as long as eye *D. (L.)* species A
4. Femora yellow 5
- At least distal $\frac{1}{2}$ of forefemur black; mid- and hindfemora mainly or entirely black 6
5. Head of male (Fig. 7) distinctly longer than high, vibrissal angle distinctly produced and antenna in deep fovea. Head of female (Fig. 8) not distinctly longer than high, vibrissal angle less produced than in male. Palpus black and enlarged in both sexes (Fig. 9). Anterior frontal seta 0.66–1.00 \times as long as posterior frontal seta *D. (L.) dolichocephala*, new species
- Head of both sexes as long as high, vibrissal angle only slightly produced in both sexes (Fig. 11). Palpus black or yellow with black tip, not enlarged. Anterior frontal seta less than half as long as posterior frontal seta *D. (L.) sabroskyi*, new species
6. Forefemur almost entirely black, only slightly yellow at base. Mid- and hindfemora entirely black. Both sexes with black enlarged palpus (as in Fig. 9) *D. (L.) nigrifemorata*, new species
- Forefemur yellow on basal 0.25–0.60, rest black. Mid- and hindfemora entirely black, or apices yellow. Palpus not enlarged, base often yellow (as in Fig. 6) 7
7. Forefemur yellow on basal 0.60. Apex of mid- and hindfemora yellow *D. (L.) glabrifrons* (Sabrosky 1965)
- Forefemur yellow on basal 0.25–0.40. Mid- and hindfemora entirely black *D. (L.) glandulifera*, new species

Desmometopa (Litometopa)
brachycephala Brake and Freidberg,
new species

(Figs. 4–6, 19–21)

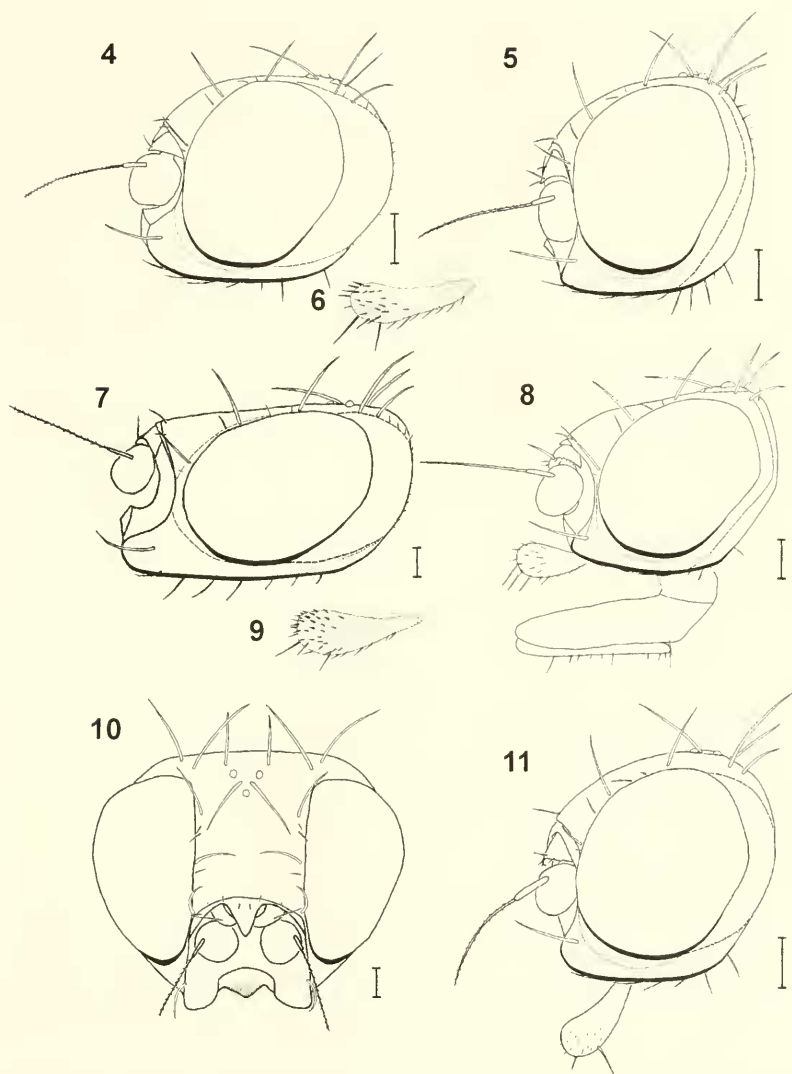
Litometopa sp. 2: Brake 2000: 11.

Diagnosis.—This species is distinguished from its congeners by the following combination of characters: Forefemur almost entirely yellow, with anterodorsal brown stripe distally; mid- and hindfemora predominantly black, apices yellow; posteroventral brush on hindtarsus yellow.

Male.—Predominantly black; forecoxa, forefemur except anterodorsal brown stripe distally, apices of mid- and hindfemora, mid- and hindtibiae, and mid- and hindtarsi except distal tarsomeres yellow. Palpus largely yellow with black tip. Posteroventral brush on hindtarsus yellow. *Head*: Anterior frontal seta about half as long as posterior frontal seta (Fig. 4). Postorbital region very long, about $\frac{1}{2}$ as long as eye. Palpus as in Fig. 6. *Wing*: Length: 1.8–2.6 mm (holotype: 2.5 mm). *Abdomen*: Tergites 1–4 microtrichose and subshiny medially, lateral and posterior margins polished; microtrichose spots progressively decreasing posteriorly, so that tergite 4 microtrichose only anteromedially or entirely polished. Tergite 5 and all sternites polished. Abdominal reservoirs present. Male genitalia as in Fig. 16.

Female (Fig. 5).—Differs from male in palpus more extensively black and slightly broadened.

Type material.—Holotype male: "UGANDA. S.W.: Fort Portal, 5 km NW, 2,000 m, 10.I.1996, I. Yarom & A. Freidberg." The holotype is double mounted, is in excellent condition, and is deposited in TAU. Paratypes: 10 σ and 3 f , same collection data as holotype (TAU, USNM). UGANDA. S.W. Kabale, 7 km NE. 1,950 m, 23.XII.1995, I. Yarom & A. Freidberg (5 σ ; TAU); Mpigi, 1,400 m, 40 km SW Kampala, 22.XII.1995, I. Yarom & A. Freidberg (2 σ ; TAU); Kisoro, 2,000 m, 26.XII.1995, I. Yarom & A. Freidberg (1 σ ; TAU). KENYA. Bungoma, 12.–



Figs. 4-11. 4-6, *Desmometopa brachycephala*. 4, Head, lateral view, male. 5, Head, lateral view, female. 6, Palpus, male. 7-10, *D. dolichocephala*. 7, Head, lateral view, male. 8, Head, lateral view, female. 9, Palpus, male. 10, Head, frontal view. 11, *D. sabroskyi*, head, lateral view, male. Scales: 0.1 mm.

13.1.1996, I. Yarom & A. Freidberg (1 ♂, forelegs missing; TAU); 10.X.1998, F Kaplan & A. Freidberg (1 ♂; TAU). ETHIOPIA. Shewa, Wendo Genet, 2,100 m, 29.1.2000, A. Freidberg & I. Yarom (6 ♂, 5 ♀; TAU, NMW.Z. BM); 1,900 m, 28.1.2000, A. Freidberg & I. Yarom (9 ♂, 3 ♀; TAU, SMNS).

Non-type material.—KENYA. West Pokot, Chepareria, 4–5.XI.1983, A. Freidberg (1 ♀; TAU). UGANDA. S.W. Ishaka, 25 km N, 1,900 m, 5.1.1996, I. Yarom & A. Freidberg (1 ♀; TAU).

Eymology.—The species name is derived from the Greek *brachys* = short and *cephalae* = head, denoting the short head.

Remarks.—The non-type female from Kenya differs from the type specimens in the black apex of the forefemur. The non-type female from Uganda was not added to the type series, because the head is shriveled.

Desmometopa (Litometopa)
dolichocephala Brake and Freidberg,
new species

(Figs. 1, 7–10, 17–18)

Litometopa sp. 1: Brake 2000: 11.

Diagnosis.—This species is distinguished from its congeners by the following combination of characters: Male with head longer than high, distinctly produced vibrissal angle, and strongly warped upward facial margin. Both sexes with anterior frontal seta 0.66–1.00× as long as posterior seta. Palpus black and enlarged. Forefemur almost entirely yellow with anterodorsal brown stripe distally; mid- and hindfemora yellow; posteroventral brush on hindtarsus dark.

Male.—Predominantly black; coxae and femora, mid- and hindtibiae and mid- and hindtarsi except distal tarsomeres yellow. *Head*: Anterior frontal seta 0.66–1.00× as long as posterior frontal seta (Figs. 7–8). Postorbital region $\frac{1}{2}$ – $\frac{1}{4}$ × as long as eye. Vibrissal angle distinctly produced anteriorly, as broad as first flagellomere, the angle em-

phasized by shiny black lateroventral corner of facial plate immediately mesad of vibrissal angle and usually warped forward and upward beyond it. Ventral margin of head comparatively long and face deeply concave as seen in profile, antenna in deep fovea. Palpus enlarged (Fig. 9). *Wing*: Length: 1.9–2.8 mm (holotype: 2.6 mm). *Abdomen*: Tergites 1–4 microtrichose and subshiny medially, lateral and posterior margins polished, microtrichose spots progressively decreasing posteriorly, so that tergite 4 is microtrichose only anteromedially. Tergite 5 and all sternites polished. Abdominal reservoirs present. Male genitalia as in Figs. 17–18.

Female.—Differs from male in head not elongated (Fig. 8) and vibrissal angle less than half as long as first flagellomere.

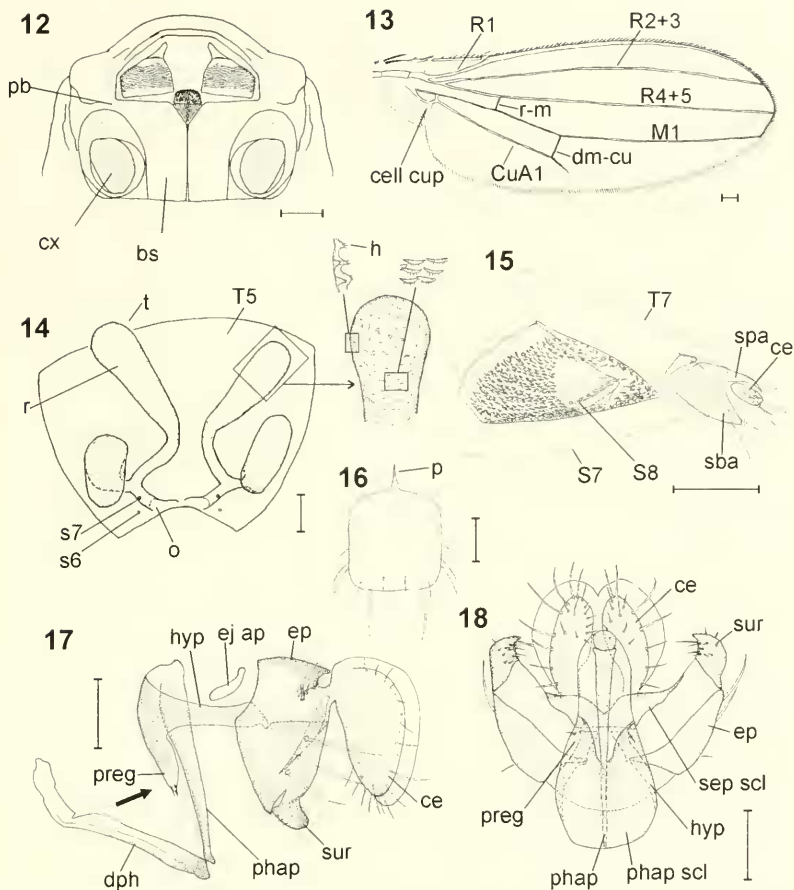
Type material.—Holotype male: "TANZANIA. Same, Rt. B1, 8–16.IX.1992, A. Freidberg." The holotype is double mounted, is in excellent condition, and is deposited in TAU. Paratypes: 9 ♂ and 1 ♀, same collection data as holotype (TAU, USNM). TANZANIA. Same, Rt. B1, 22.VIII.1996, A. Freidberg (2 ♂; TAU); 8.IX.1996, A. Freidberg (7 ♂, 1 ♀; TAU, HU).

Eymology.—The species name is derived from the Greek *dolichos* = long and *cephalae* = head, denoting the particularly long head of the male.

Desmometopa (Litometopa) flavicornis
Brake and Freidberg, new species

Diagnosis.—This species is distinguished from its congeners by the following combination of characters: First flagellomere in male yellowish medially and at extreme base, dark only around base of arista; forefemur in both sexes almost entirely yellow, with anterodorsal brown stripe distally; mid- and hindfemora yellow; posteroventral brush on hindtarsus yellow.

Male.—Predominantly black; forecoxa, forefemur except anterodorsal brown stripe distally, mid- and hindfemora, mid- and hindtibiae, and mid- and hindtarsi except distal tarsomeres yellow. Palpus yellow



Figs. 12–18. 12. *Desmometopa sabroskyi*, prothorax, ventral view (from Brake 2000), bs—basis sternum, cx—base of coxa, pb—precoccal bridge. 13–14. *Desmometopa* sp. A, male. 13. Wing (from Brake 2000), CuA— anterior cubitus, cell cup—posterior cubital cell, dm-cu—discal medial-cubital crossvein, M—media, R—radius, r-m—radial-medial crossvein. 14. Abdominal reservoirs, ventral view, h—setulae on indentations, r—reservoir, t—tissue, o—opening, s—spiracle, T—tergite. 15–16. *D. sabroskyi*, female. 15. Tip of ovipositor with secondary ovipositor inverted, lateral view (from Brake 2000), ce—cerci, S—sternite, sba—subanal plate, spa—supra-anal plate, T—tergite. 16. Sternite 6 (from Brake 2000), p—process at anterior margin. Scales: 0.1 mm. 17–18. *D. dolichocephala*, male terminalia. 17. Lateral view. 18. Viewed in direction of black arrow in Fig. 17. Scales: 0.1 mm.

with light brown to brown tip. Posteroventral brush on hindtarsus yellow. *Head*: Anterior frontal seta half as long as posterior frontal seta. Postorbital region about $\frac{1}{6} \times$ as long as eye. Palpus as in Fig. 6. *Wing*: Length: 2.1–2.5 mm (holotype: 2.2 mm). *Abdomen*: Tergites 1–5 microtrichose and subshiny medially, polished laterally. Abdominal reservoirs present. Male genitalia as in Fig. 17.

Female.—Differs from male in entirely black first flagellomere. Palpus black except mesobasally.

Type material.—Holotype male: "NIGERIA: Ife, 2 Aug. 1969/J. T. Meddler Coll." The holotype is double mounted, is in excellent condition, and is deposited in the USNM. Paratypes: 2 ♂ and 2 ♀, same collection data as holotype (USNM). NIGERIA, Niger State: Mariga River, 80 km NW Minna, 11.XII.1987, Fini Kaplan (1 ♀; TAU).

Etymology.—The species name is derived from the Latin *flavus* = light and *cornus* = horn, denoting the yellowish first flagellomere of the males.

Desmometopa (Litometopa) glabrifrons
(Sabrosky), **new combination**

Litometopa glabrifrons Sabrosky 1965: 4.

Diagnosis.—This species is distinguished from its congeners by the following combination of characters: Basal $\frac{1}{3}$ of forefemur yellow, remainder black; mid- and hindfemora black, except for apices; posteroventral brush on hindtarsus dark; male without abdominal reservoirs.

Male.—Predominantly black; basal $\frac{1}{3}$ of palpus, forecoxa, basal $\frac{1}{3}$ of forefemur, apices of mid- and hindfemora, mid- and hindtibiae and mid- and hindtarsi except distal tarsomeres yellow. *Head*: Anterior frontal setae half as long as posterior frontal seta. Postorbital region $\frac{1}{5}$ – $\frac{1}{6}$ as long as eye. Palpus as in Fig. 6. *Wing*: Length: 2.2–2.6 mm (holotype: 2.6 mm). *Abdomen*: Tergites 1–4 microtrichose and subshiny medially, polished laterally, microtrichose spots pro-

gressively decreasing posteriorly; tergite 5 and all sternites polished. Abdominal reservoirs absent, but small base of ducts present (in dissections of paratype and non-type material). Male genitalia as in Fig. 17.

Female.—Differs from male in basal half of palpus yellow and palpus slightly broader.

Type material.—The holotype male bears several labels: "O. Afrika, T. T. Marangu, 1.–20. Maerz 1959, Lindner leg." On the lower side of the label the date is specified as "17.III." The second label reads "Holotype, *Adesmometopa glabrifrons*, male, C. W. Sabrosky." The third label says "*Adesmometopa glabrifrons*, det. Sabrosky." The fourth label reads "*Litometopa glabrifrons* Sabrosky." The second and third labels were probably written by Sabrosky himself and indicate that he first considered naming the genus *Adesmometopa*. However, in his description he named the genus *Litometopa* and therefore the correct name is stated on the fourth label, which was probably not written by Sabrosky himself. The holotype is double mounted, is in good condition except for the slightly shriveled head, and is deposited in the SMNS. One male paratype bears the first label with the same data as the holotype but with "10.III." on the lower side (USNM). The second label says "Paratype, *Litometopa glabrifrons*, male, C.W. Sabrosky," and the third label reads "*Litometopa glabrifrons*, det. Sabrosky." For the other two original paratypes see below.

Additional specimens examined.—TANZANIA. Marangu, E. Lindner, 10.III.1959 (1 ♀; SMNS). SOUTH AFRICA. Natal, Uvongo, South Coast, 11.X.1983, A. Freidberg (2 ♂, 1 ♀; TAU); North Transvaal, Tzaneen, 1977, Van Eeden, at *Euphorbia* flowers (1 ♀; USNM). KENYA (West). Kapenguria—Tartar Road, 24.XI.1989, A. Freidberg & F. Kaplan (1 ♀; TAU). ETHIOPIA. Shewa, Wendo Genet, 1.900 m, 28.I.2000, A. Freidberg & I. Yarom (1 ♂; TAU); 2,100 m, 29.I.2000, A. Freidberg & I. Yarom (2 ♂; TAU).

Remarks.—Two of the original paratypes, one male and one female (allotype), were found not to be conspecific with the holotype and are redescribed below as *D. sabroskyi*. These two specimens differ from the holotype of *D. glabrifrons* by the yellow mid- and hindfemora and the almost entirely yellow forefemur with an antero-dorsal brown stripe distally.

One male from South Africa, Natal, Uvongo, differs from the holotype in the forefemur being black on the distal half posteriorly and distal $\frac{2}{3}$ anteriorly and in the shape of the head, which is similar to *D. brachycephala*. The female from South Africa, North Transvaal, differs from the holotype in the black apices of the mid- and hindfemora. These specimens nevertheless are considered variants of *D. glabrifrons*.

Desmometopa (Litometopa) glandulifera
Brake and Freidberg, new species

Diagnosis.—This species is distinguished from other congeners by the following combination of characters: Basal $\frac{1}{4}$ – $\frac{2}{5}$ of forefemur yellow, rest black; mid- and hindfemora black; posteroventral brush on hindtarsus dark.

Male.—Predominantly black; forecoxa, basal $\frac{1}{4}$ – $\frac{2}{5}$ of forefemur, mid- and hindtibiae and mid- and hindtarsi except distal tarsomeres yellow. Mid- and hindtibiae in some specimens quite dark. Palpus brown with darker tip, but in some specimens palpus mesobasally yellow. *Head*: Anterior frontal seta half as long as posterior frontal seta. Postorbital region $\frac{1}{6}$ – $\frac{1}{5}$ × as long as eye. Palpus as in Fig. 6, in some specimens slightly narrower. *Wing*: Length: 1.9–2.4 mm (holotype: 2.4 mm). *Abdomen*: Tergites 1–4 microtrichose and subshiny medially, polished laterally, microtrichose spots progressively decreasing posteriorly; tergite 5 and all sternites polished. In some specimens anterior margin of tergite 5 subshiny. Abdominal reservoirs present. Male genitalia as in Fig. 17.

Female.—Does not differ from male ex-

cept for the usual differences between male and female.

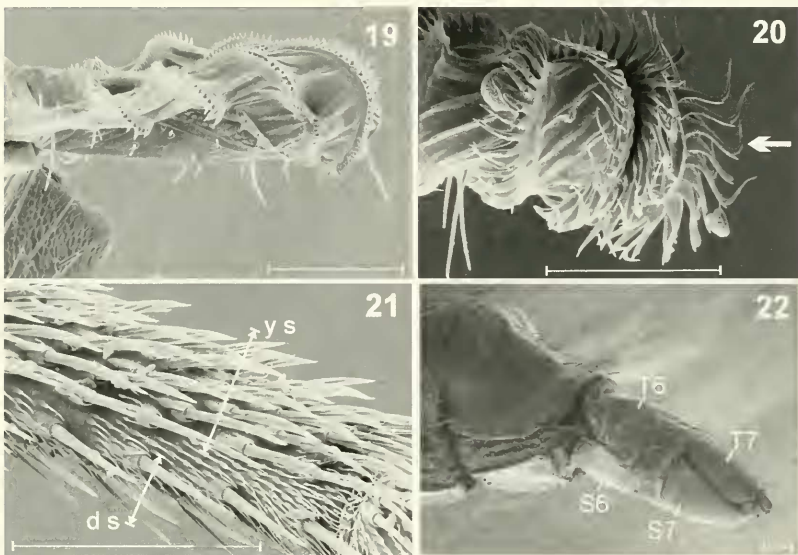
Type material.—Holotype male: "ETHIOPIA: Shewa, Wendo Genet, 1,900 m, 28.I.2000, A. Freidberg & I. Yarom." The holotype is double mounted, is in excellent condition, and is deposited in TAU. Paratypes: 3 ♂ and 1 ♀, same collection data as holotype (TAU, USNM). ETHIOPIA. Shewa, Wendo Genet, 2,100 m, 29.I.2000, A. Freidberg & I. Yarom (1 ♂; TAU); Gamo, Gofa, 3 km NE Arba Minch, 1,300 m, 'Forest', 5.II.2000, A. Freidberg & I. Yarom (1 ♀; TAU). KENYA. Bungoma, 12.–13.I.1996, I. Yarom & A. Freidberg (1 ♀; TAU). KENYA. Kabarnet, 11.–12.X.1998, F. Kaplan & A. Freidberg (1 ♂; TAU); Tsavo West, Ngulia Lodge, 16.–17.VIII.1983, A. Freidberg (1 ♀; TAU). RWANDA. Rusumu, Ibanda Makera, 2°09'S/30°55'E, 1,350 m, canopy fogging on *Teclea nobilis*, gallery forest; 7.XI.1993, Th. Wagner, stored in ethanol (X 1006-T.n.5, 1 ♀; X 1006-T.n.6, 1 ♂; X 1006-T.n.8, 1 ♂; X 1006-T.n.10, 1 ♂) (ZSM, ZFMK, UBI). TANZANIA. Lugoba, Rt B 1218, 25.VIII.1996, A. Freidberg (3 ♂, 1 ♀; TAU); Manga, Rt. B1218, 6.IX.1996, A. Freidberg, on mango, (1 ♂; TAU).

Etymology.—The species name is derived from the Latin *glands* = gland and *ferre* = carry, bear, denoting the abdominal reservoirs.

Desmometopa (Litometopa) nigrifemorata
Brake and Freidberg, new species

Diagnosis.—This species is distinguished from its congeners by the following combination of characters: Both sexes with entirely black and enlarged palpus; forefemur black except for base; mid- and hindfemora black; posteroventral brush on hindtarsus dark.

Male.—Predominantly black; forecoxa, base of forefemur, mid- and hindtibiae and mid- and hindtarsi except distal tarsomeres yellow. Palpus black. *Head*: Anterior frontal seta half as long as posterior frontal seta. Two setulae between frontal setae. Length



Figs. 19–22. SEM, 19–21. *Desmometopa brachycephala*. 19. Labella, lateral view, male. 20. Tip of labella, lateral view, female. 21. First tarsomere of hindleg, female, y s—yellow setae, d s—dark setae. 22. *D. sabroskyi*; ovipositor, lateral view (from Brake 2000). S—sternite, T—tergite. Scales: 0.1 mm.

of postorbital region not recognizable because of shriveled head. The same holds true for the vibrissal angle. Palpus as in Fig. 9. *Wing*: Length: 2.5–2.6 mm (holotype: 2.6 mm). *Abdomen*: Tergites 1–4 microtrichose and subshiny medially, polished laterally, microtrichose spots progressively decreasing posteriorly; tergite 5 and all sternites polished.

Female.—Differs from male in slightly narrower palpus. In female from Uvongo, anterior frontal seta about $\frac{3}{4}\times$ as long as posterior frontal seta.

Type material.—Holotype male: "SOUTH AFRICA: Natal. Uvongo, South Coast, 11.X.1983, A. Freidberg." The holotype is double mounted, is slightly shriveled, and is deposited in TAU. Paratypes: 1 ♀, same collection data as holotype (TAU). SOUTH AFRICA. Itala Game Reserve, 27°30'S/31°20'E, 27.–29.I.1994, U. Göllner (1 ♀; HU).

Etymology.—The species name is derived from the Latin words *niger* = black and *femur* = thigh, femur, denoting the black femora.

Desmometopa (Litometopa) sabroskyi
 Brake and Freidberg, new species
 (Figs. 11–12, 15–16, 22)

Litometopa ?*glabrifrons*: Brake 2000: 11 (in part).

Diagnosis.—This species is distinguished from its congeners by the following combination of characters: Forefemur almost entirely yellow with anterodorsal brown stripe distally; mid- and hindfemora yellow; posteroventral brush on hindtarsus dark.

Male.—Predominantly black; fore- and hindcoxae, forefemur except anterodorsal brown stripe distally, mid- and hindfemora, mid- and hindtibiae, and mid- and hindtarsi except distal tarsomeres yellow. Palpus yellow.

low with dark tip or entirely dark. *Head*: Anterior frontal seta less than half as long as posterior frontal seta. Postorbital region moderately long, $\frac{1}{6}$ – $\frac{1}{5}$ × as long as eye (Fig. 11). *Wing*: Length: 1.8–2.0 mm (holotype: 2.0 mm). *Abdomen*: Tergites 1–4 microtrichose and subshiny medially, polished laterally; tergite 5 and all sternites polished.

Female.—Does not differ from male except for the usual differences between male and female.

Type material.—Holotype ♂: "UGANDA: S.W. Fort Portal, 5 km NW, 2,000 m, 10.I.1996, I. Yarom & A. Freidberg." The holotype is double mounted, is in excellent condition, and is deposited in TAU. Paratypes: 1 ♂, same collection data as holotype (TAU); 1 ♀, same collection data but "7.I.1996" (TAU), NIGERIA, Ife, 2. Aug. 1969/J. T. Meddler Coll. (3 ♀; USNM). UGANDA. S.W. Kabale, 7 km NE, 1,950 m, 23.XII.1995, I. Yarom & A. Freidberg (1 ♀; TAU); District Masindi, Budongo Forest, N'River Sonso, 1°45'N/31°25'E, 1,200 m, canopy fogging on *Cynometra alexandri* (C.a.) and *Rinorea beniensis* (= *ardisiifolia*) (R.a.), seasonal rain forest, 19.VI.–31.VII.1995, Th. Wagner, stored in ethanol (X 1259-C.a.3, 2 ♀; X 1259-C.a.16, 1 ♀; X 1259-R.a.1, 2 ♀, X 1259-R.a.3, 3 ♀; X 1259-R.a.7, 1 ♀; X 1259-R.a.12, 1 ♀; X 1259-R.a.13, 1 ♀; X 1259-R.a.15, 1 ♀; X 1259-R.a.16, 1 ♀) (ZSM, ZFMK, UBI). CONGO. Kivu-Sud, Irangi, 1°54'S/28°27'E, 950 m, canopy fogging on *Carapa grandifolia*, rain forest, 7.XI.1993, Th. Wagner, stored in ethanol (X 1006-C.g.5, 6, 15, 18, 1 ♀) (ZSM). TANZANIA. Marangu, 3.III.1959, E. Lindner (1 ♂, 1 ♀, para- and allotype of *D. glabrifrons*, Sabrosky, SMNS).

Etymology.—This species is named in memory of Curtis W. Sabrosky, a friend and dipterist, who dominated the taxonomic study of Milichiidae in the twentieth century and described the genus *Litometopa*.

Remarks.—The female from Uganda, Kabale differs from the holotype in the slightly broader palpus. The male and fe-

male from Tanzania, Marangu, and one female from Nigeria, Ife, differ from the holotype in the dark apex of the forefemur.

Desmometopa (*Litometopa*), species A
(Figs. 13–14)

Litometopa ?*glabrifrons*: Brake 2000: 11 (in part).

These specimens differ from *D. flavicornis* in the shape of the head in male. Postorbital region in male short. Palpus nearly yellow in male, black except for medial base in female, and slightly broader than in male. Mid- and hindfemora yellow to light brown. The females cannot be differentiated from the females of *D. flavicornis*.

Material examined.—UGANDA, District Masindi, Budongo Forest, N'River Sonso, 1°45'N/31°25'E, 1,200 m, canopy fogging on *Rinorea beniensis* (R.a.) and *Teclea nobilis* (T.n.), seasonal rain forest; 19.VI.–31.VII.1995, Th. Wagner, stored in ethanol (X 1259-R.a.3, 4 ♀; X 1259-R.a.17, 1 ♀; X 1259-T.n.12, 2 ♂; X 1259-T.n.13, 1 ♀) (ZSM).

Remarks.—We refrain from naming this species, because there are just two males, which are very similar to *D. flavicornis*, so that species A might just be a variant or subspecies of the latter species. The above listed females cannot be differentiated from the females of *D. flavicornis*, and therefore cannot give support for naming species A.

ACKNOWLEDGMENTS

We are grateful to M. Balke, Dr. K. Kiontke, Prof. Dr. W. Sudhaus, and Dr. W. N. Mathis for reviewing a draft of this paper. We thank Dr. L. Cederholm of the Entomologica Scandinavica Supplements for the permission to use the figures 1, 7, 10, 12–13, 16, and 22 from Brake (2000).

LITERATURE CITED

- Brake, I. 2000. Phylogenetic systematics of the Milichiidae (Diptera, Schizophora). Entomologica Scandinavica Supplement 57: 1–120.
 Cumming, J. M., B. J. Sinclair, and D. M. Wood. 1995. Homology and phylogenetic implications of male

- genitalia in Diptera—Eremoncira. *Entomologica Scandinavica* 26: 120–151.
- Hennig, W. 1973. 31. Diptera (Zweiflügler). *Handbuch der Zoologie* 4(2), 2/31 (Lfg. 20): 1–337.
- McAlpine, J. F. 1981. Chapter 2. Morphology and terminology: adults, pp. 9–63. *In* McAlpine, J. F. et al., eds, *Manual of Nearctic Diptera*, Vol. 1. Research Branch, Agriculture Canada, Monograph 27. Ottawa, vi + 1–674 pp.
- Meier, R. and K. Dettner. 1998. The ultrastructure of a rectal gland in the Sepsidae and the composition of its secretion. 4th International Congress of Dipterology, 6.–13. Sept. 1998, Oxford, Abstract Vol.: 143–144.
- Sabrosky, C. W. 1965. East African Milichiidae and Chloropidae (Diptera). *Stuttgarter Beiträge zur Naturkunde* 138: 1–8.
- . 1983. A synopsis of the world species of *Desmometopa* Loew (Diptera, Milichiidae). *Contributions of the American Entomological Institute* 19(8): 1–69.
- Smith, K. G. V. and R. G. Davies. 1965. Glandlike abdominal structures of possible epigamic function in the Diptera. *Nature* 4994: 321–322.
- Speight, M. C. D. 1969. The prothoracic morphology of acalyptrates and its use in systematics. *Transactions of the Royal entomological Society of London* 121: 325–421.
- White, I. M., D. H. Headrick, A. L. Norrbom and L. E. Carroll. 2000. 33 Glossary, pp. 881–924. *In* Aluja, M. and A. L. Norrbom, eds. *Fruit Flies (Tephritidae): Phylogeny and Evolution of Behaviour*. CRC Press, Boca Raton.